

Ant colony size and the scaling of reproductive effort

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Summary

1. Reproductive effort typically scales as $mass^{0.75}$ in unitary organisms, but less is known about such scaling in colonial organisms.
2. I compiled data on worker and reproductive number at maturity for 65 ant species and found an interspecific allometry ($alate\ number = worker\ number^{0.73}$) whose exponent was significantly < 1 , even after a phylogenetic correction.
3. When I analyzed 15 species for which biomass data were available, I found an interspecific isometry ($alate\ biomass = worker\ biomass^{0.89}$) whose exponent was not significantly different from 1. Analysis of maximum species biomass values, rather than averages, strengthened this isometry, yielding a slope $b = 1.01$ that was also not distinguishable from 1.
4. Species with larger colony size at reproduction tended to couple investment in proportionately fewer alates with investment in larger male and female alates.
5. This comparative analysis suggests a trade-off between alate size and number, and provides a framework for studying the diversity of colony life histories and the mechanisms generating allometries.

Key words: colonial organism, life-history trade-off, sex allocation conflict, unitary organism

Introduction

From an organism's body size, it is possible to accurately predict many aspects of its physiology (Kleiber 1932; Brown *et al.* 2004), ecology (Brooks & Dodson 1965; Peters 1983; Kaspari 1993) and life history (Blueweiss *et al.* 1978; Sibly & Brown 2007). An important correlate of body size is that females of larger species tend to invest proportionately less energy in their offspring per unit time (Reiss 1989). Measures of reproductive output typically scale as a power law (aM^b), where $b < 1$ (Blueweiss *et al.* 1978; Sibly & Brown 2007), and data from unitary organisms (*colonies of cells*) suggest that reproductive allometry arises from metabolic allometry (Brown & Sibly 2006). Interestingly, colonial organisms (*colonies of individuals*) show similar patterns (Michener 1964; Hughes & Hughes 1986; Karsai & Wenzel 1998) despite some evidence that larger colonies do not have metabolic constraints (Lighton 1989; Martin 1991). Colonial organisms may instead face unique constraints on reproductive allocation and provide insights into the causes of whole-organism scaling (Glazier 2005; Edmunds 2006). To date, however, interspecific analyses of colony size and the scaling of reproductive effort have been lacking (Tschinkel 1991).

Ant (Hymenoptera: Formicidae) colonies provide a model system for comparative life-history studies because they include *c.* 12 000 species (Bolton *et al.* 2006), and reproduce at sizes spanning over half the range of all animals (10^{-5} to 10^9 g; Kaspari & Vargo 1995). Like unitary organisms, ant colonies make decisions about when to reproduce, and how much of a limited resource pool to allocate to reproduction (Pamilo 1991; Backus 1995; Herbers, DeHeer & Foitzik 2001). Although alternative strategies exist (e.g. Peeters 1991), colonies of most species *grow* by allocating energy to the production of sterile workers that care for developing brood, defend the nest and harvest resources from the environment (Oster & Wilson 1978). Colonies *reproduce* when they allocate these resources to sexual alates that disperse, mate and found new colonies (Oster & Wilson 1978). Since Michener (1964) empirically found a social insect reproductive allometry, theory has sought to explain how the advantages of large colony size compensate for the corresponding decrease in reproductive output per worker (Wenzel & Pickering 1991; Naug & Wenzel 2006). Even so, few have tested whether this pattern applies across social insect taxa (but see Karsai & Wenzel 1998).

Here, I first quantify the scaling of reproductive effort across the ants. I supplement this with a phylogenetic analysis using independent contrasts to examine the relationship between the evolution of larger colony size and reproductive

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effort (e.g. Warton *et al.* 2006). Correcting for phylogeny removes the statistical problem of non-independence among closely related species (Harvey & Pagel 1991). Agreement between methods may also bolster interpretations of the scaling of life-history variables (Berrigan *et al.* 1993).

I next contrast the scaling of alate size and number, because evidence suggests a trade-off observed for unitary organisms (Lack 1954; Smith & Fretwell 1974; Stearns 1992), also applies to ant colonies (Rosenheim, Nonacs & Mangel 1996). First, reproduction is costly to colonies because alates are generally larger and contain more energy than workers (Peakin 1972). Reproducing colonies further divert resources to alates at the expense of workers that decline in both mass and number (Tschinkel 1987, 1993). Second, colonies benefit from investing more per alate because alates are typified by high mortality rates (Tschinkel 1992; Frederickson 2006) and a positive relationship between size and fitness (Davidson 1982; Wiernasz & Cole 2003; Fjerdingstad & Keller 2004). I test the prediction that larger colonies package proportionately equivalent mass into relatively fewer alates, such that numerical allometry ($b < 1$) will be offset by biomass isometry ($b = 1$).

The scaling of ant colony reproductive effort may also be shaped by unique genetic and ecological factors (Herbers 1990; Pamilo 1991; Sundstrom 1995; Ruppell, Heinze & Holldobler 2001; Fjerdingstad 2005; Linksvayer 2006). Unlike cells in a body, individuals in a colony are not genetically identical, and the resulting relatedness asymmetries (RA) cause conflict over reproductive allocation (Hamilton 1964; Trivers & Hare 1976). RA may shape reproductive scaling because its strength depends on aspects of colony structure that may vary with colony size, such as queen number (mono- vs. polygyny), queen mating frequency (mono- vs. polyandry) and worker reproduction (Trivers & Hare 1976; Herbers 1990; Keller & Vargo 1993; Crozier & Pamilo 1996). For example, colonies of sterile workers headed by a single, once-mated queen have high RA and are predicted to bias investment towards female alates (Boomsma & Grafen 1990; Chapuisat & Keller 1999). Because female alates are generally larger than male alates (e.g. Herbers 1984), increasing RA with colony size would generate numerical allometry with larger colonies packaging resources as fewer, larger female alates. To test for systematic changes in sex allocation with colony size, I contrast the scaling of male and female alate number and size.

Measurements of reproductive allocation may also depend on how colonies spread reproductive effort throughout their life. Annual colonies are semelparous and do not divide investment between current and future reproduction (Oster & Wilson 1978; Pamilo 1991; Herbers *et al.* 2001). Mature annual colonies may thus allocate relatively more to reproduction for their size than perennial colonies. Unfortunately, limited data availability precludes comparative analyses of the effects of lifetime reproductive schedules. I focus instead on seasonal reproductive phenology, because this also shapes how colonies spread reproductive effort across time. I contrast the scaling of temperate species (that tend to release alates in

single, pulsed flights; Dunn *et al.* 2007) and tropical species (that tend to release alates gradually, over longer periods; Kaspari, Pickering & Windsor 2001).

Combined, these comparative analyses fill gaps in the study of social insect life history and facilitate comparison with unitary organisms. Scaling may also reveal constraints on life-history evolution (e.g. Brown & Sibly 2006), and thus inform theoretical predictions regarding how genetic and environmental factors shape colony phenotypes.

Methods

I examined the interspecific scaling of reproductive effort by combining colonies collected from a tropical forest in Panama during the summers of 2005–2007 with a literature review (> 250 articles). I sought studies reporting both alate output (number or dry biomass) and colony size (worker number or total worker dry biomass) (see Appendix S1 in the Supplementary material). For five species, I pooled data from multiple studies (see Supplementary Appendix S1). Because sampling limitations may affect the precision of colony size estimates, I applied the following criteria for data selection. I generally avoided estimates without methods and those not published in peer-reviewed journals. I focused on estimates of worker and alate number determined from whole colony collections, and generally avoided mark and recapture data, the results of manipulative field and laboratory experiments and longitudinal studies. I assumed equal probabilities of underestimating worker number (e.g. some foragers will have in the field when the nest was harvested) and alate number (e.g. some may have dispersed before the nest was harvested).

I defined colony size as the total number and, when available, total biomass of adult workers. I defined reproductive output as alate number and, when available, biomass. I computed both mean and maximum values when articles provided a range of values. Analysing maximum values may better represent a reproductive constraint by showing the upper limits on reproductive effort (Tschinkel 1993; Porter & Hawkins 2001). Some species have colonies with ambiguous boundaries because they simultaneously nest in multiple, spatially discrete sites (e.g. polydomy; see review Debout *et al.* 2007). Removing the data of known polydomous species ($N = 15$ species; determined from the citations in Supplementary Material Appendix S1 and Debout *et al.* 2007), however, did not change the results. To further control for variation due to polydomy, I only used data from my collections if colonies were monodomy and had a queen. I also avoided published data from extremely polydomous species (e.g. *Formica yessensis*; Higashi & Yamauchi 1979).

I used least square regression to estimate a and b in the scaling equation $\log_{10} y = \log_{10} a + b \log_{10} M$. Scaling characterized the dependence of reproductive output (*alate number* or *dry biomass*; y) on colony size (*worker number* or *total worker dry biomass*; M). To detect allometry ($b \neq 1$), I calculated an F -statistic to test the null hypothesis of isometry ($H_0: b = 1$). Testing different hypotheses required slopes from separate analyses of how \log_{10} (worker number) shaped 7 measures of reproductive effort (Table 2). I therefore used a Bonferroni correction to adjust the significance level for these comparisons at 0.007 (0.05/7). For all measurements of colony size and reproductive output, I calculated $\text{pWR} = \log_{10}(M_{\text{max}}/M_{\text{min}})$ as a standard measure of size range (Prothero 1986). I analyzed the scaling of sexual allocation (males vs. females) and region (temperate vs. tropical) with ANCOVA. For analysis by region, I used locality information within articles to assign species to temperate (> 23°

Table 1. Summary statistics for species averages of linear measurements. The measure $pWR = \log_{10}(\text{max value}/\text{min value})$ is a standardized measure of the size range. *denotes dry biomass (mg) – otherwise, values are numbers of individuals

Level	Species	Genera	Worker values		Alate values	
Alate number	65	35	Mean	17 671	Mean	345
			Range	18–650 000	Range	2–4673
			pWR	4.61	pWR	3.4
Alate biomass	15	8	Mean	5714*	Mean	1632*
			Range	0.88–34 385*	Range	0.08–17 738*
			pWR	4.59*	pWR	5.35*
Male number	52	29	Mean	25 207	Mean	407
			Range	19–775 000	Range	1 4880
			pWR	4.61	pWR	3.69
Female number	51	27	Mean	6432	Mean	154
			Range	17–109 143	Range	1–1560
			pWR	3.81	pWR	3.19
Male size	29	15	Mean	5688	Mean	2.43*
			Range	24–58 112	Range	0.035–10.6*
			pWR	3.38	pWR	2.48*
Female size	29	16	Mean	7129	Mean	10.59
			Range	14–58 112	Range	0.09–59.5*
			pWR	3.62	pWR	2.82*

latitude) or tropical ($< 23^\circ$) groups (as per Kaspari & Vargo 1995; see Supplementary Appendix S1). For analyses of sex allocation and colony size, I used queen number data from the original citation and other published accounts if necessary (see Supplementary Appendix S1). Where relevant, I also used SMATR software (Warton *et al.* 2006) to test for differences in the intercept of regression lines if slopes were found to be not significantly different. This method uses ANOVA on residual scores as a test for common intercept of regression lines (Warton *et al.* 2006).

I further removed phylogenetic non-independence from the comparative analysis using Comparative Analysis by Independent Contrasts (CAIC software by Purvis & Rambaut 1995) and the molecular phylogeny of the ants by Brady *et al.* (2006). CAIC tests hypotheses of correlated evolution using evolutionary relationships (the topology) and distances (branch lengths) from a phylogeny to calculate standardized contrasts for pairs of sister species (e.g. estimating the trait value of the common ancestor) that can then be subjected to traditional statistical tests (Purvis & Rambaut 1995). I set branch lengths to 1, assuming a punctuated model of evolution (Harvey & Pagel 1991) and grouped congeners as soft polytomies, analyzing them as single comparisons. Data were \log_{10} transformed prior to calculation of contrasts, assuming that different lineages were equally likely to make the same proportional changes in size (Purvis & Rambaut 1995). The scaling of contrasts was analyzed using linear regression through the origin because this forces the regression line to include both the point of no evolutionary divergence and the centre of standardized data (Warton *et al.* 2006).

Results

The scaling of alate number included 65 ant species from 35 genera, with worker number spanning 4.6 orders of magnitude (18–650 000) and alate number spanning 3.4 orders of magnitude (2–4,673) (Table 1). *Alate number* scaled as *worker number*^{0.73} ($R^2 = 0.78$; Fig. 1) and was significantly less than isometry (F -test for $b = 1$: $F_{1,63} = 29.9$, $P = 0.0001$; Table 2). Analysis using maximum values instead of averages, did not change the result ($b = 0.78$, $R^2 = 0.76$; F -test for $b = 1$:

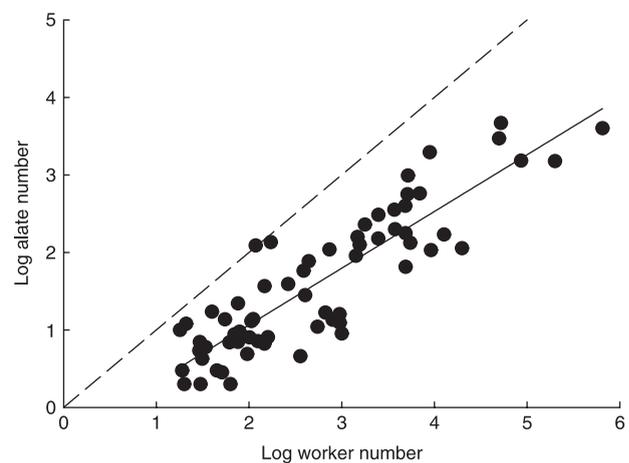


Fig. 1. Log-transformed relationship between alate number and worker number. Dashed line represents isometry. Each data point represents a species average.

$F_{1,63} = 15.3$, $P = 0.0002$; Table 2). This allometry remained significant after a phylogenetic analysis with independent contrasts ($R^2 = 0.75$, $F_{1,42} = 124.8$, $P = 0.0001$; Fig. 2) and was significantly less than isometry (F -test for $b = 1$: $F_{1,42} = 46.3$, $P = 0.0001$; Table 1).

The scaling of alate biomass included 15 ant species from eight genera, with worker biomass spanning 4.6 orders of magnitude (0.88–34 385 mg) and alate biomass spanning 5.4 orders of magnitude (0.08–17 738 mg) (Table 1). *Alate biomass* scaled as *worker biomass*^{0.89} ($R^2 = 0.95$; Fig. 3) and was not significantly different from isometry (F -test for $b = 1$: $F_{1,14} = 3.70$; $P = 0.08$; Table 2). This two-tailed test of H_0 : $b = 1$, however, included only 15 species and thus had low power (power = 0.50, Zar 1999; p. 385). Further analysis using maximum values strengthened the isometric relationship ($b = 1.01$, $R^2 = 0.96$; F -test for $b = 1$: $F_{1,14} = 0.050$, $P = 0.830$; Table 2).

Table 2. Least squares mean regression for scaling relationships. For regressions of alate output against \log_{10} (worker number), deviation from isometry ($b = 1.0$) denoted by * ($P < 0.007$), the critical value set by a Bonferroni adjustment (see Methods). *Avg.* and *Max.* refer to average and maximum species values. The *biomass* regressions denote the analysis of summed alate vs. summed worker biomass and used a critical value 0.05. *CAIC* is the phylogenetically independent contrasts regression, and its parameters have been calculated with the intercept (a) set to 0 (see Methods)

Group	<i>N</i>	MS model	MS error	<i>F</i>	<i>R</i> ²	<i>a</i>	SE	<i>b</i>	SE	±95% CI
Numerical avg.	65	40.63	0.182	223.0	0.780	-0.400	0.145	0.73*	0.049	0.098
Numerical max.	65	45.00	0.231	195.0	0.756	-0.311	0.170	0.78*	0.056	0.113
CAIC	43	4.283	0.034	124.8	0.748	0.000	n/a	0.62*	0.056	0.111
Biomass avg.	15	31.46	0.121	260.2	0.952	-0.379	0.141	0.89	0.055	0.120
Biomass max.	15	38.14	0.122	313.2	0.960	-0.453	0.153	1.01	0.057	0.124
Male number	53	32.34	0.142	228.2	0.817	-0.441	0.147	0.72*	0.048	0.095
Female number	52	18.42	0.241	86.23	0.633	-0.061	0.182	0.58*	0.063	0.126
Male size	29	2.148	0.060	35.68	0.569	-0.407	0.137	0.28*	0.047	0.096
Female size	29	5.498	0.116	47.40	0.637	-0.430	0.179	0.41*	0.059	0.121

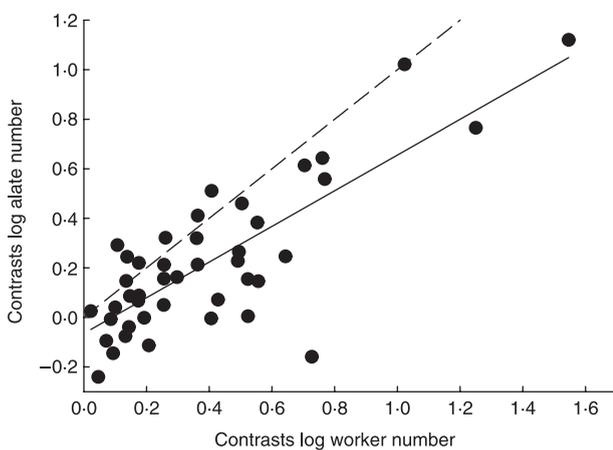


Fig. 2. Log-transformed relationship between alate number and worker number using phylogenetically independent contrasts. See Methods for details.

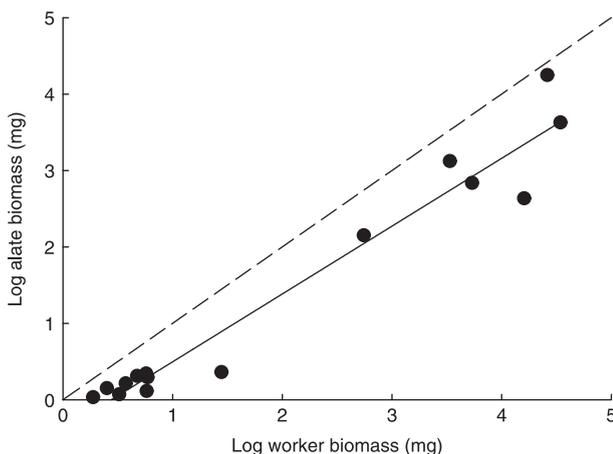


Fig. 3. Log-transformed relationship between total alate dry biomass and total worker dry biomass. Dashed line represents Isometry. Each data point represents a species average.

Tschinkel (1993; fig. 25) also scaled the reproductive biomass of six ant species and found that maximum values supported isometry. These results suggest that alate number accumulates more slowly with colony size than total mass. In other words,

larger colonies tend to package proportionately equivalent mass into relatively fewer alates.

To analyze how sex allocation shapes reproductive scaling, I first quantified the scaling of male and female alate number. Data from most of the 65 species included colonies producing both alate sexes and the scaling of male and female number included averages from 53 male producing species and 52 female producing species ($N = 105$), with some species being used for both analyses. Male and female alate numbers were regressed against average worker numbers using only colonies producing that sex. Although alate number generally increased with worker number ($P = 0.0001$), the relative number of male and female alates did not change ($P = 0.108$) (Table 3). The scaling of *female number* = *worker number*^{0.58} ($R^2 = 0.633$; Fig. 4a) and *male number* = *worker number*^{0.72} ($R^2 = 0.817$; Fig. 4b) were not significantly different ($P = 0.0850$; Table 3). After removing the interaction term, alate sex remained non-significant ($F_{2,102} = 0.001$, $P = 0.99$).

Table 3. Comparing the scaling of alate number and alate size against worker number for male and female alates and across regions. The result of ANCOVAs using worker number as a covariate

Effect	Factor	df	Type III SS	<i>F</i>	<i>P</i> > <i>F</i>
Alate number	\log_{10} (worker number)	1	49.22	277	0.0001
	Alate sex	1	0.467	2.63	0.1077
	\log_{10} (worker number) × sex	1	0.535	3.02	0.0850
	Error	101			
Alate size	\log_{10} (worker number)	1	7.094	80.5	0.0001
	Alate sex	1	0.001	0.01	0.9200
	\log_{10} (worker number) × sex	1	0.250	2.83	0.0980
	Error	54			
Region	\log_{10} (worker number)	1	36.89	229	0.0001
	Region	1	0.457	2.84	0.0970
	\log_{10} (worker number) × sex	1	0.054	0.34	0.5640
	Error	61			

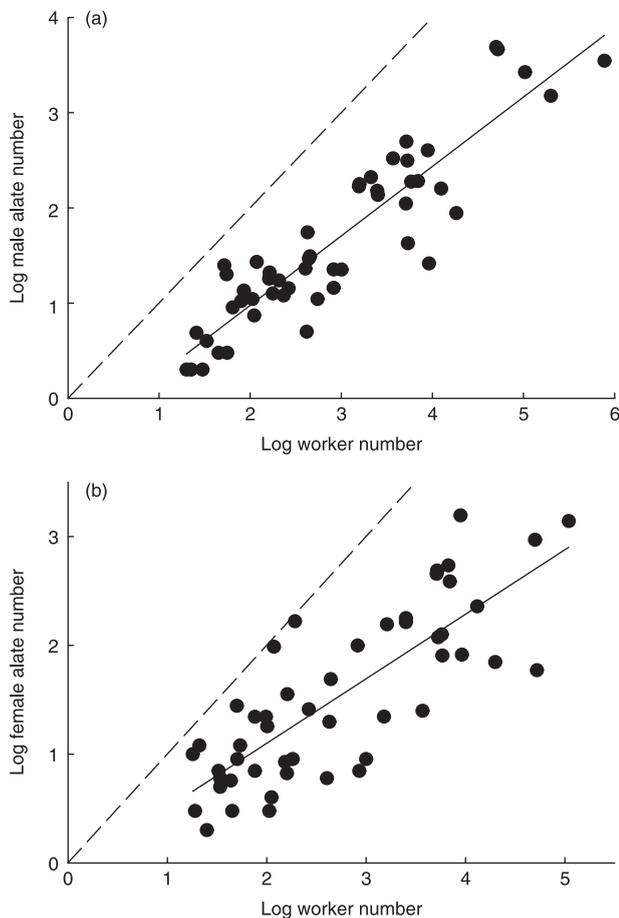


Fig. 4. (a) Log-transformed relationship between male alate number and worker number. (b) Log-transformed relationship between female alate number and worker number.

To gather sufficient data to analyze the scaling of male and female size with worker number, I combined published accounts of alate dry biomass with conspecific colony size estimates (see Appendix S2 in the Supplementary material). Average alate size generally increased with worker number ($P = 0.0001$), but it did not vary between sexes ($P = 0.920$) (Table 3). The scaling of *male size* = $worker\ number^{0.28}$ ($R^2 = 0.569$; Fig. 5a) and *female size* = $worker\ number^{0.41}$ ($R^2 = 0.637$; Fig. 5b) were not significantly different (Table 3). After removing the non-significant interaction term, however, females tended to be larger than males ($F_{1,55} = 18.08$, $P = 0.0001$; least square means of log alate biomass: female = 0.710, male = 0.373). The intercept of the regression for female size was significantly greater than the intercept for male size ($F_{1,28} = 11.7$, $P = 0.001$).

I next examined the effects of region. Alate number tended to increase with worker number ($P < 0.0001$), although neither tropical nor temperate colonies tended to have more alates ($P = 0.097$) (Table 3). The scaling of temperate ($alate\ number = worker\ number^{0.68}$, $R^2 = 0.695$) and tropical ($alate\ number = worker\ number^{0.73}$, $R^2 = 0.853$) species was not significantly different (Table 3). This result suggests that reproductive scaling does not result from sampling colonies with different phenologies.

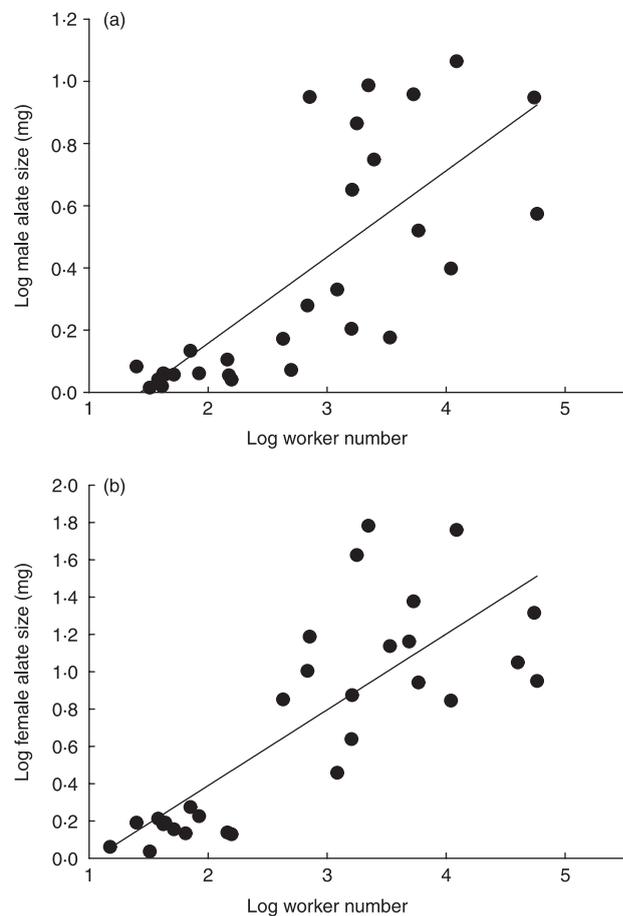


Fig. 5. (a) Log-transformed relationship between individual male alate biomass and worker number. (b) Log-transformed relationship between individual female alate biomass and worker number.

Discussion

Large ant colony size may enhance the ability to discover and defend resources (Wenzel & Pickering 1991; Holway & Case 2001; Palmer 2004), confer protection against adverse environmental conditions (Kaspari & Vargo 1995), and facilitate increasingly complex colony-level behaviours (Beckers *et al.* 1989; Gordon 1995; Pacala, Gordon & Godfray 1996; Karsai & Wenzel 1998; Anderson & McShea 2001). This comparative analysis provides support for an additional benefit – the production of larger alates (Fig. 5a,b). Numerical allometry (Figs 1 and 2) and biomass isometry (Fig. 3) suggest that species maturing at larger colony sizes tend to package proportionately equivalent mass into relatively fewer alates. This correlation suggests a reproductive trade-off – that alate size and number compete for the allocation of limited resources (Stearns 1992).

The trade-off between alate number and size may depend on which resource limits parental investment (Rosenheim *et al.* 1996). Alate size may also be constrained by a combination of environmental and genetic effects (Fjerdingstad 2005). Colonies may further allocate to alates based on fixed schedules of development (Backus 1995) or by weighing

the benefits of current and future reproduction against a backdrop of sex allocation conflict (Pamilo 1991; Herbers *et al.* 2001). This comparative analysis supports the notion that these factors are constrained in a general way by colony size (Tschinkel 1993). Deviation above or below the general allometry may represent the fitness consequences of ecological innovation (e.g. Sibly & Brown 2007). For example, if polydomy reduces foraging costs by placing nest fragments closer to resources (van Wilgenburg & Elgar 2007), polydomous species may have relatively more energy for reproduction than predicted from their colony size. This analysis also facilitates comparison of lineages with different life histories. The subfamily Ponerinae contains *c.* 100 species whose colonies lack queens and instead have mated, egg-laying workers (Peeters 1991). In these colonies, physical conflicts over who reproduces (Heinze, Holldobler & Peeters 1994) may divert energy from reproduction to posturing behaviours (Gobin *et al.* 2003).

These analyses did not detect systematic changes in sex allocation. First, the relative number of male and female alates did not change with colony size (Table 3). Second, female alates were generally larger than males, but they did not become increasingly so with increasing colony size (Table 3). Although comparative analyses provide limited insights into how RA shapes sex allocation conflict (Boomsma 1989), relatedness within colonies may nevertheless vary as species mature at larger colony sizes. Interestingly, although queen number may increase with colony size within facultatively polygynous species (Elmes & Keller 1993; Sundstrom 1995), a logistic regression of monogynous and polygynous colonies within this data set did not find a significant relationship with colony size (Wald statistic = 2.77, $P = 0.1$, $df = 1$). Further comparative studies will be needed to determine whether the evolution of larger colony size increases the probability of polyandry (Cole 1983; Crozier & Fjerdingstad 2001; Kronauer, Johnson & Boomsma 2007) and worker reproduction (Herbers 1990; Snyder & Herbers 1991; Crozier & Pamilo 1996).

The effects of ecological constraints on reproductive scaling remain uncertain. If large colonies are better equipped to discover and defend resources (e.g. Holway & Case 2001), they may be able to invest in relatively more expensive female alates (Nonacs 1986; Peterson & Roitberg 2006). Alternatively, due to limitations of central place foraging, larger colonies may increasingly deplete local resources (Oster & Wilson 1978) causing workers to make longer, more energetically expensive foraging trips (Fewell *et al.* 1996). If these workers yield diminishing returns per foraging trip, larger colonies may have proportionately fewer resources available for reproduction. The ecology of resource harvesting may be further complicated by interactions between the scaling of worker size and colony size (e.g. Bourke 1999) because larger workers tend to have greater foraging efficiency (Davidson 1978; Kaspari 1993). These dynamics may be offset by systematic changes in foraging strategies with colony size (Beckers *et al.* 1989).

Scaling from colonial organisms may also help evaluate models predicting that metabolic constraints unify diverse

taxa (Glazier 2005). Biologists have long sought to explain why metabolic rate (I) scales with body mass as a quarter power ($I = M^{0.75}$) from the smallest microbes (10^{-14} g) to the largest homeotherms (10^7 g) (West, Brown & Enquist 1997; Brown *et al.* 2004; Glazier 2005). This metabolic allometry may constrain the life histories of unitary taxa because the proportionately slower metabolic rate of larger species limits the rate they allocate resources to reproduction (Brown & Sibly 2006). Larger ant colonies may also have proportionately slower metabolic rates because, like larger unitary organisms, they tend to yield proportionately fewer reproductive individuals (Figs 1 and 2). Similar constraints may be expected because unitary and colonial organisms are both composed of highly interdependent life-forms that behave as a single organism (e.g. ant workers in ant colonies, Queller & Strassmann 2002; host and microbial cells in metazoan bodies, Sekirov & Finlay 2006). Furthermore, whole-organism metabolic scaling for both these biological types arises from how the numbers, sizes and metabolic rates of their subunits (e.g. cells or workers) scale with body (Savage *et al.* 2007) or colony (Lighton 1989) size. It remains unclear, however, whether colony-level energetics represents the allometric decline in per-worker respiration ($b < 1$; Galle 1978; Bartholomew, Lighton & Feener 1988), or the additive sum of worker respiration ($b = 1$; Lighton 1989; Martin 1991).

Colony life-history data have been published for relatively few of the *c.* 12 000 known ant species (Tschinkel 1991; Kaspari & Vargo 1995). Of those species for which data exist, we have much to learn regarding how colony attributes change during colony development and throughout a colony's lifetime (Wilson 1985). The preceding analyses suggest strong colony-size dependence of important life-history traits despite the limited availability and variable precision of colony-level data. Nevertheless, some important implications of these analyses remain to be fully explored. For instance, although female size increased faster with worker number ($b = 0.41$) than male size ($b = 0.28$), the slopes were not significantly different (Table 3). A trade-off should favour ever-greater investment in females relative to males because female size may be more closely tied to fitness (Rosenheim *et al.* 1996). This is because female traits relate to how they disperse (Nonacs 1993) and found new colonies (Keller & Passera 1989; Stille 1996; Johnson 2002; Hahn *et al.* 2004), while males have few sexually selected traits and die shortly after mating (Boomsma, Baer & Heinze 2005). The scaling approach used here provides a framework for such analyses as data continue to become available.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Data used for scaling. Abbreviations: $\log w \# = \log_{10}(\text{worker number} + 1)$, $\log(a \#) = \log_{10}(\text{alate number} + 1)$, $\log(wbm) = \log_{10}(\text{summed dry worker biomass} + 1)$, $\log(abm) = \log_{10}(\text{summed dry alate biomass} + 1)$. All measurements dry biomass in mg. N signifies number of colonies in the sample. TE refers to temperate region ($> 23^\circ$ latitude), TR refers to tropical region ($< 23^\circ$ latitude). $Q \#$: queen number for colonies used in this analysis ($1 = 1$ queen, $2 \geq 1$ queen, $B =$ both 1 and multiply queened colonies)

Appendix S2. Data used to scale individual male and female biomass with worker number. Abbreviations: $\log w \# = \log_{10}(\text{worker number} + 1)$, $\log(mbm) = \log_{10}(\text{individual male biomass} + 1)$, $\log(fbm) = \log_{10}(\text{individual female biomass} + 1)$. All measurements dry biomass in mg. If alate biomass source different from worker number source: *Trivers & Hare (1976), ^Keller & Passera (1989)

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